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Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species

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Abstract

Sex-biased survival linked to anthropogenic threats places populations at risk. We show the utility of long-term multi-decadal photo-id combined with long-term high resolution (Fastloc-GPS) satellite telemetry to investigate the links between mortality rates and patterns of movement for a wide-ranging, endangered marine vertebrate. Using a photo-identification database of 947 loggerhead turtles (*Caretta caretta*) compiled over 18-years, we estimated greater annual survival rates of females (0.89; 95% CI 0.87–0.90) compared to males (0.73; 95% CI 0.67–0.78). For males satellite-tracked across multiple breeding seasons, 100% (26 of 26) returned to the same breeding site, suggesting the calculated lower male survival-rate was likely not due to emigration to breed elsewhere. 10,111 and 2,524 tracking days for males (n=39 individuals) and females (n=18 individuals), respectively, revealed different habitat-use patterns outside the breeding season: males tended to occupy foraging sites closer to shore and closer to breeding sites but, due to their generally annual breeding, compared to biennial breeding for females, males migrated further per year on average. These differences in movement patterns likely contribute to higher mortality in males through increased interaction with anthropogenic threats. Long-term identification coupled with tracking offers great promise for estimating the survival rates of other wide-ranging species.

Key words: migration, conservation, ageing; life-history traits; life-span; mark-recapture; population dynamics; rate of living theory

Introduction

Adult survival rates may be closely linked to population status and drive population trajectories, and so are of great interest particularly for long-lived, slow to mature endangered species (Wittemyer et al. 2014, Cano et al. 2016). Consequently, there has been huge effort to estimate adult survival rates across a range of species, and this is often achieved by marking individuals and then looking at patterns of re-sighting over time within a classical capture-mark-recapture framework (Schwarz et al. 2013, Ward et al. 2018). However, for some species marking individuals is not straightforward, such as cetaceans and some large fish (e.g. manta rays) that are difficult or impossible to directly handle. In these cases, photo-id may provide a more reliable method for long-term identification (Deakos et al. 2011, Kanive et al. 2015, Sprogis et al. 2016, Pace et al. 2017). For example, photo-id has been used to estimate that the population of adult right whales in the North Atlantic numbers only a few hundred, and that in recent years individuals have suffered high mortality rates (Pace et al. 2017).

While a capture-mark-recapture approach can reveal survival rates, this approach may not reveal where mortality is occurring for many groups, including both terrestrial and marine taxa. Yet, patterns of movement influence the susceptibility of animals to both natural and anthropogenic mortality by dictating the magnitude of interactions with various threats (Fossette et al. 2014, Frick et al. 2017). Consequently, identifying the magnitude of these threats remains a central goal of many studies (Hays et al. 2016, Kanive et al. 2019). For example, a group that attracts both huge conservation effort and concern is sea turtles, where adults face a number of threats, including direct capture for human consumption, incidental capture (bycatch) through various fishing activities, and mortality through boat strikes (Rees et al. 2016, Frick et al. 2017). For adults, there is a huge dichotomy in our understanding of adult females, which emerge on to sandy beaches to nest where they can be readily observed and tagged, versus adult males, which generally do not come ashore and so are far harder to study (Rees et al. 2016). Hence, while mark-recapture studies using numbered flipper tags or injected Passive Integrated Transponder (PIT) tags have been used to estimate the survival rates of adult females nesting at sites around the world (Pfaller et al. 2018), there are far fewer estimates of survival rates for adult males. This lack of knowledge about adult males is now particularly worrying since there are growing concerns that around the world hatchling sex ratios are heavily biased to females due to the combination of temperature-dependent sex determination and warm, female-producing sand temperatures dominating nesting beaches (Hawkes et al. 2009, Poloczanska et al. 2009).

Given this broad concern about adult survival rates and increasingly female-skewed sex ratios in sea turtles in the face of climate change, here we set out to use a unique multi-decadal photo-id database at a globally important breeding area to assess survival rates for both adult males and females. In addition, we used extensive long-term high resolution (Fastloc-GPS) satellite telemetry to investigate the links between mortality rates and patterns of movement. We thus illustrate how the synergy of these two techniques, photo-id and satellite tracking, can be used to tackle a topic of very wide interest and topicality.

Methods

Study site

The study was conducted in the NATURA 2000 submerged shallow sandbank habitats of Laganas Bay, within the National Marine Park of Zakynthos on Zakynthos Island, Greece (37°43' N, 20° 52' E) (Appendix S1: Fig. S1). The bay is 106 km^2 in size and contains six discrete loggerhead sea turtle nesting beaches, supporting 833−2018 nests (Casale and Margaritoulis, 2010) made by around 166−403 females yr^{-1}, assuming each female lays five clutches, or 277−672 females yr^{-1}, assuming each female lays three clutches each season (Schofield et al. 2017).

Field surveys

In water surveys were conducted across the same range of dates each year, namely in April, May and June from 2000 to 2017. Surveys were regularly distributed on fair weather days, which occurred frequently (21 ± 2 days/month on average) across the three months, to ensure survey effort (and hence detection probability) was similar for males (primarily present in April and May) and females (primarily present in May and June). The survey area extended up to 400 m offshore along an 8 km section of coastline where male and female turtles have been confirmed to aggregate based on the tracking data (loggers and transmitters) of over 100 individuals (Schofield et al. 2013a; Appendix S1: Fig. S1). Surveys were conducted by swimming or from small vessels (kayak or 4-m motorized boat), moving parallel to shore along transect lines set 100 m apart running parallel to shore until turtles were sighted, at which point, observers either swam towards the turtles to take photos (at 2 to 7 m distance from the target animal, depending on underwater sea visibility) or obtained photographs from the vessels (Schofield et al. 2008). There were one to three observers (the same observers across years). Still and video photographs of the facial scutes (left, right, top) and body parts were taken with a succession of digital camera technology over the

18-year period. External signs of disturbance of our presence (photographs required <1 min) were negligible as observations were normally for >2 min (Schofield et al. 2008).

Photo-identification database

Individuals were identified using photo-identification (Fig. 1; and Schofield et al. 2008), in which size class, estimated sex and resident/migrant status were documented. The database was compiled manually using a key to separate individual turtles into groups based on facial (post-ocular) scale patterns to facilitate rapid comparison of new images in the catalogue of known turtles. This matching process was validated by using turtles marked with external flipper tags (Schofield et al. 2008) and each unique individual in the database was confirmed by two of the authors (Gail Schofield and Kostas Papafitsoros). Immature turtles were identified as individuals that were smaller than the minimum expected breeding curved carapace length (CCL) for loggerheads at the site, based on the random capture of adult male (n = 45 unique individuals) and female (n = 43 unique individuals) turtles within the breeding area from 2006 to 2012 (Schofield et al. 2017; range: 71–102 cm for males; 74–96 cm for females), supporting data obtained by Margaritoulis et al. (2003) for nesting females (range: 70–96.5 cm; n = 395 individuals). For males, these designations were also validated at the study site, as several resident individuals exhibited tail-elongation as they matured over successive years (Appendix S1: Fig. S2). Immature turtles were removed from the data set and not considered in the survival analysis.

To assess the longest re-sighting interval, we supplemented the photo-id data with information from external flipper tags that were originally attached on the nesting beaches by ARCHELON (Sea Turtle Protection Society of Greece) and were present during the earliest photo-identification records, but were subsequently lost. In these cases, the photo-id could be spliced with the original flipper tagging year using the annual flipper tag letter codes reported in Lazar et al. (2004).

Local survival and re-sighting probability

Adult survival rate (Φ) and recapture rate (p) were estimated using Bayesian Population Analysis (Kery and Schaub 2012). Survival and recapture rate were calculated separately for males and females over either a 1-year or a 2-year evaluation period (i.e., four different models). The models in which we used a 1-year period for males and a 2-year period for females were considered the most realistic, as most males have annual return rates, while most females have

biennial return rates in the study population (Hays et al. 2014). For the modelling, we used a script adapted from a published script in Chapter 7.3 (Kery and Schaub 2012) and for each population model, we conducted 20 Markov chain Monte Carlo (MCMC) simulations using 10,000 iterations. Initial parameters were chosen randomly for each MCMC simulation. The last 5,000 iterations were used to describe the posterior distribution of each parameter (i.e., their median and 95% confidence interval), and to calculate the model's goodness of fit. For the latter, the Deviance Information Criterion or DIC was used, where lower values indicate better fits. Out of the 20 MCMC simulations, the simulation with the lowest DIC was ultimately used. For the accuracy of Φ and p estimation $\hat{R}$ was used, with values of $\hat{R}$ close to 1 identifying good fits. The CMR model allowed us to estimate both the survival rates separately for males and females, in addition to the recapture rates; thus, the model allows for the detectability of males and females to be different. Because surveys were consistent across years, we assumed that variation in recapture rates, re-sighting probability and detectability was negligible.

Site fidelity and mortality rates based on Argos-linked Fastloc-GPS

We used data from 57 loggerhead sea turtles equipped with high-resolution Argos-linked Fastloc-GPS units to help establish fidelity to the Zakynthos breeding area and to identify foraging grounds outside the breeding season and infer mortality. The units were attached between 2007 and 2012, primarily in May before the onset of nesting activity (seven to 22 units were attached per year; for details, see Schofield et al. 2013a,b). To evaluate differences in migratory distances between foraging and breeding grounds for males and females, we included distance data from 18 additional females tracked by Zbinden et al. (2011) between 2004 and 2006. Mortality events were either reported to us when dead turtles were found and/or inferred from an anomalous pattern of locations relayed from satellite tags (Hays et al. 2007), with tags showing movement to shore and then remaining stationary in the littoral zone, indicative of turtle death. We also used photo-id records to confirm the lack of mortality in a number of turtles where transmitters stopped. Furthermore, we examined the extent of coastal development adjacent to foraging destinations (http://planbleu.org; five-point scale) and the proximity of foraging sites to the coastline (using the central location within previously calculated home ranges (Dujon et al. 2018). Foraging sites were delineated by the displacement distance from the previous site remaining constant for at least 6-days and travel speed decreasing to <1 km/h (Schofield et al. 2013b). Some turtles use multiple foraging sites; however, our tracking data showed that turtles return to the same primary foraging

site following migration from breeding sites, with just five turtles shifting between coastal and oceanic sites; thus, only the primary foraging site was used for this analysis. For 18 previously published tracks (Zbinden et al. 2011), the distance of foraging sites from the shore was not available.

Results

Overview of the Photo-ID database

A total of 947 uniquely identified loggerhead sea turtles (adult male, 147; adult female, 773; immature turtle, 27) were documented from 2000 to 2017. However, the sample size used to calculate survival and recapture rate were lower and dependent on the length of the evaluation period (i.e. one or two years), since animals sighted for the first time in the last observation period were excluded from the Bayesian Population Analysis.

Most females bred biennially (193 out of 527 recorded breeding intervals, while most males bred annually (84 out of 108 recorded breeding intervals). Annual (79 out of 527 recorded breeding intervals) and triennial (95 out of 527 recorded breeding intervals) remigration of females was also documented. For both females and males, we assumed those resighted with intervals of longer than 3 years had been missed breeding in the interim.

Annual survival rates

All models yielded accurate parameter estimates, $\hat{R}$ between 1 and 1.01 (for details see Appendix S1: Section S1, Supplementary Results). Almost identical parameter estimates were obtained across the 20 iterations for each model. Given the >1-year breeding cycle of females, it is most appropriate to compare models estimating local annual survival and recapture rate over 1-year periods in males and 2-year periods in females. This model gave annual survival rates for males of 0.73 (95% CI 0.67–0.78) and 0.89 for females (95% CI 0.87–0.90) (Appendix S1: Fig. S3). This sex-bias in survival estimated from the models was also readily evident in simple examination of the empirical data at four-year intervals (i.e., allowing for at least two remigrations) (Fig. 2, paired t-test $P > 0.05$ between modelled and empirical data for both sexes). For instance, for turtles sighted at the start of our time-series that could conceivably have been sighted 15 or more years later, only 3 males and 8 females were seen again after this amount of time.

However, there were occasional records of individuals being sighted over longer periods. For example, for one male, sightings records extend from 2000 to 2018, suggesting at least 18 years as a mature individual. For five females, the external flipper tags (originally attached on the nesting beaches that were present during their earliest photo-identification records (but subsequently lost, with photo-id being used to connect records to present) indicated re-sighting records since at least 1991 up to 2018 giving at least 27 years as mature individuals.

Foraging grounds, site fidelity, and mortality

Fastloc-GPS tracking data were obtained for 10,111 and 2,524 tracking days for males (n=39 individuals) and females (n=18 individuals) respectively. Fifty-four turtles were tracked until after the initial breeding season had ended and 52 were tracked to foraging sites. Overall, turtles travelled to sites up to 1,537 km distance from Zakynthos, with males migrating a mean of 608 km (SD ± 468 km) and females migrating a mean of 796 km (SD ± 301 km). However, while two males migrated the longest distances of all individuals (over 1500 km to the west Mediterranean), significantly more males migrated to foraging grounds closer to the breeding area (of which seven were resident and two more remained within 100 km) compared to females (one remained within 100 km, not resident) (Kruskal-Wallis test = 4.1308, $P < 0.05$). Foraging sites were distributed up to 200 km from shore, with mean distances of 21 km (±34) and 28 km (±40) for males and females respectively; however, 56 and 57% of males and females, respectively, actually frequented sites within 10 km of shore. Of importance, 38% of tracked males occupied habitat within 1 km of shore versus just 7% of females, with this difference being highly significant (Kruskal-Wallis test = 7.6174, $P < 0.01$) (Fig. 3). There was no difference in the level of coastal development at these sites between males and females (70% of both males and females frequented sites near low coastal development).

Our calculated survival rate is composed of actual survival plus emigration. So, in theory, the male/female differences in calculated survival rate might be because males tend to have lower breeding site fidelity and instead a greater tendency to emigrate to alternate breeding sites across years. However, satellite tracking results suggest this was not the case. For example, we satellite tracked 26 male turtles for >9 months, of which 100% returned to breed on Zakynthos either in the subsequent year (n = 22) or the year after (n = 4). While mortality may often go unreported, in three instances we obtained evidence of mortality of tracked individuals either from direct observation and/or from relayed tracking data. All three cases were for males. One male died

while the transmitter was still operational in the second year of tracking (Appendix S1: Fig. S4) and the unit was retrieved from the individual (resident to Zakynthos Island) when tracking data showed the animal moving and remaining ashore for several weeks; one died after transmission failure <9 months after deployment, with the animal being found three months later dead in the Ionian Sea on the island of Kefalonia; mortality of the third turtle was inferred from the transmission signals, following a similar pattern to the first turtle with the transmitter coming ashore and then no detected movement for multiple days (Amvrakikos Delta, Greece). The two dead turtles found at Zakynthos and Kefalonia had evidence of propeller damage on their carapaces, and the one from Zakynthos had also ingested a fishing hook and line.

Discussion

Our study shows the utility of long-term photo-id coupled with tracking to identify survival rates and threats to migratory species. Hence, this approach may have broad utility across taxa. Importantly, through combining these approaches, we showed that sex-biases in survival rates appear linked to sex-biases in movement. One possible explanation for the male/female difference in survival rate is increased investment in reproduction by males as documented for other taxa (Clutton-Brock et al. 2002, Lemaitre et al. 2015). However, this seems not to be the case with sea turtles since, during a breeding year, males spend less time than females away from their foraging sites and hence are able to spend longer replenishing their energy reserves after breeding (Hays et al. 2014). Furthermore, as well as reduced time on the foraging grounds during a breeding year, females also invest heavily in the structural content of eggs, with several hundred eggs being laid over a nesting season. Hence, we need to look for other potential reasons to explain the observed female/male difference in survival rates.

Another possibility is that sex-biases in survival are linked to differences in movement patterns and, hence, levels of threat. Similarly, sex-biased mortality linked to movements has recently been identified in various seabirds (Cortes et al. 2018, Yamamoto et al. 2019). Previous studies tracking male turtles also demonstrated that foraging sites were coastal (van Dam et al. 2008, Arendt et al. 2012), although the exact proximity to shore of the foraging grounds were not reported. Our tracking data supports the idea that adult male turtles breeding in Greece suffer higher anthropogenic mortality rates. Compared to females, males occupied foraging sites closer to the breeding area, in addition to frequenting areas much closer to shore. This difference in space use may expose males to greater anthropogenic threats, including boat strike from recreational

activities and/or local fisheries (Hazel et al. 2007, Frederiksen et al. 2015). Elsewhere in the world, propeller strikes have been identified as an important cause of mortality for sea turtles (Wallace et al. 2013) and other taxa (e.g., whale strikes; Monnahan et al. 2015) and have led, for example, to restrictions on boat speeds or changing shipping routes (Hazen et al. 2018). While satellite tracking will not always indicate when an animal has died, for example tags may fail for a number of reasons (Hays et al. 2007), and so may not reveal mortality rates, the cases of mortality we found in tracked animals supported this idea that boat strikes are an important threat. Also, adult males breed more frequently than females, both in Greece and likely elsewhere (Hays et al. 2014). This difference in breeding intervals means that males will spend more time than females migrating, rather than being in relatively fixed locations on either the breeding or foraging areas. Assuming males and females migrate 1,216 and 1,592 km to and from foraging grounds on average (608 km and 796 km one way), respectively, with 1.2 and 2.04 year remigration intervals (based on the photo-identification database), males travel 30% further than females per year on average (1013 versus 780 km per year, respectively). During migration, turtles are more likely to encounter anthropogenic threats that occur in the open ocean, such a longline fishing (Lewison et al. 2004, Wallace et al. 2013). Hence this increased time spent migrating may also contribute to the lower male survival rates that we reported.

Exposure to different types and intensities of anthropogenic threats (Halpern et al. 2008, Lutcavage et al. 2013) may also contribute to the differences in survival rates reported for adult female sea turtles at different breeding and foraging sites globally. For example, for loggerhead turtles, annual survival rates ranging from 0.73 to 0.91 have been reported around the globe (Pfaller et al. 2018). Previously extensive mark-recapture data and robust statistical modelling have been used to show that, for loggerhead and green turtles on the Great Barrier Reef, there were no sex specific differences in survival (Chaloupka 2002, Chaloupka and Limpus 2002, 2003). So, the differences we report in survival between adult males and females in Mediterranean, likely a consequence of their different movement behaviors, might not be a universal trait. Therefore, it is important that future work around the world determines whether sex specific survival exists at particular sites and the broader implications, for example in terms of climate change and changing hatchling sex ratios. Sea turtles exhibit temperature-dependent sex-determination, and there is widespread concern that climate warming will cause increasingly female-biased hatchling sex ratios, since females are produced at warmer temperatures (Hays et al. 2017). Hence, in a warming world, adult male turtles may become increasingly scarce and may

ultimately threaten population viability [46]. Therefore, the lower adult male survival that we reported may increasingly threaten populations under scenarios of climate change. So, while our methods (in water photo-identification and longer-term tracking of males) are often more taxing than simply tagging females when nesting ashore, we urge others to invest in assessing adult male survival rates. Indeed, learning more about male turtles has been identified as one of the key questions for sea turtle biology in general (Jensen et al. 2018). Other potential approaches that could be used to distinguish sexes and unique individuals, aside from those we used, include underwater submersibles (ROVs, Smolowitz et al. 2015), drones (Schofield et al. 2019), or by identifying unique individuals through genetic microsatellites (Vieira et al. 2016). Increased knowledge of how turtle movements impact their survival will also help ongoing efforts to translate tracking data into conservation policy and management (Rees et al. 2016, Hays et al. 2019).

As a general paradigm, immature turtles shift from more oceanic to coastal foraging habitats as they mature, with some exceptions (Bjorndal 1997). Of note, when compared to the estimated annual survival rates for immature turtles in the Mediterranean (0.73, Casale et al. 2007), our rates for adult males were equivalent (0.73), but were noticeably higher for females (0.89). It might be expected that, as turtles grow and mature, their annual survival rate might increase as they are less susceptible to natural predators (Heppell et al. 2000), and this seems to be the case for females in the Mediterranean. However, the similar survival rates for immature turtles versus adult males, suggests that any increased survival for males due to increased size is counterbalanced by their change in habitat use. Similarly, differences in life-history traits between adult males and females of other taxa contribute to the observed sex-specific differences in survival (Weimerskirch et al. 1997, Frederiksen et al. 2005, Xavier et al. 2005). For instance, Kanive et al. (2015, 2019) reported a male biased adult sex ratio in white sharks (*Carcharodon carcharias*) and suggested this finding may be the result of differential male/female mortality earlier in life or emigration of females. These studies highlight the importance of research on the potential causes of sex ratio bias across species.

In captivity, it is sometimes estimated that sea turtles can live for >50 years. For example, a captive green turtle (*Chelonia mydas*) that has been housed at a New England (USA) Aquarium since the 1960s, and that is still alive, has been estimated to be at least 70 years old (personal communication Kara Dodd and Charles Innes). So, it appears that sea turtles may be able to live for decades, but this longevity appears to be very rarely achieved for loggerhead turtles breeding

in Greece. The proportion of individuals surviving x years after their initial sighting may be calculated as ASR^x, where ASR = the annual survival rate. So based on our estimated annual survival rates, the proportion of individuals surviving x years after their initial sighting was 0.73^x for males and 0.89^x for females. For example, the proportion of males and females surviving 10 and 20 years after their initial sighting was 0.043 (i.e. 4.3%) and 0.002 (i.e. 0.2%), respectively, for males and 0.312 (i.e. 31.2%) and 0.097 (i.e. 9.7%), respectively, for females. Given that the age to reach maturity for loggerhead turtles in the Mediterranean is estimated to be around 18 years (Casale et al. 2011) it is likely that few adult turtles reach an age of 40 years. Our annual survival estimates fall broadly within the range reported for loggerhead sea turtles across 23 sites by (Pfaller et al. 2018), suggesting that limited longevity of free-living sea turtles may apply broadly. Compared to captive animals, free-living turtles face increased physiological challenges such as searching for food and performing long-distance migration during which they fast (Hays et al. 2016). Free-living individuals are exposed to natural predators (e.g. sharks), as well as suffering anthropogenic mortality, e.g. through targeted capture, bycatch in fisheries and boat strikes (Lutcavage et al. 2013, Wallace et al. 2013). It may be that this combination of physiological challenges and mortality threats constrain the longevity of free-living individuals. Across species it is well known that longevity scales with body size, with larger animals tending to live for longer (deMagalhaes and Costa 2009, Healy et al. 2014), and also varies across taxa (e.g. between mammals, reptiles, birds etc.; Healy et al. 2014, Sabath et al. 2016). So perhaps the most similar species with which to compare the longevity of sea turtles are giant Galapagos tortoises (*Chelonoidis negra*), which are well known to live for >100 years in the wild (deMagalhaes and Costa 2009, Healy et al. 2014), which contrast markedly with our estimates of longevity for sea turtles. Of note here, is that Galapagos tortoises have no natural predators when adults and certainly nowadays are relatively easy to protect because of their limited movements compared to sea turtles.

Our estimated limited longevity of sea turtles suggests that a large proportion of their lives may be spent reaching sexual maturity. For example, assuming our longest records for the period of maturity (26 years; Jensen et al. 2018) and a minimum maturation time of 18 years (Casale et al. 2011), we estimate that >40% of the free-living life-span for a loggerhead turtle is spent attaining sexual maturity. This value for loggerhead turtles is towards the upper limits of the range for reptiles (e.g. 43% for the red-bellied black snake; deMagalhaes and Costa 2009), as well as being generally much higher than the mean values reported for varied taxa including for mammals

(8%), birds (10%), reptiles (16%), amphibia (21%), and teleost fishes (25%), but is similar to the mean values for cartilaginous fishes (42%) (deMagalhaes and Costa 2009). This relatively short period of sexual maturity poses conservation challenges for sea turtles, since the life-time of reproductive output of individuals will be less than might be expected based on their long-time taken to reach sexual maturity. These findings reiterate the importance of efforts of conservation efforts to reduce anthropogenic mortality to sea turtles. This is particularly important in light of climate change impacts which threaten the feminization of sea turtle populations.

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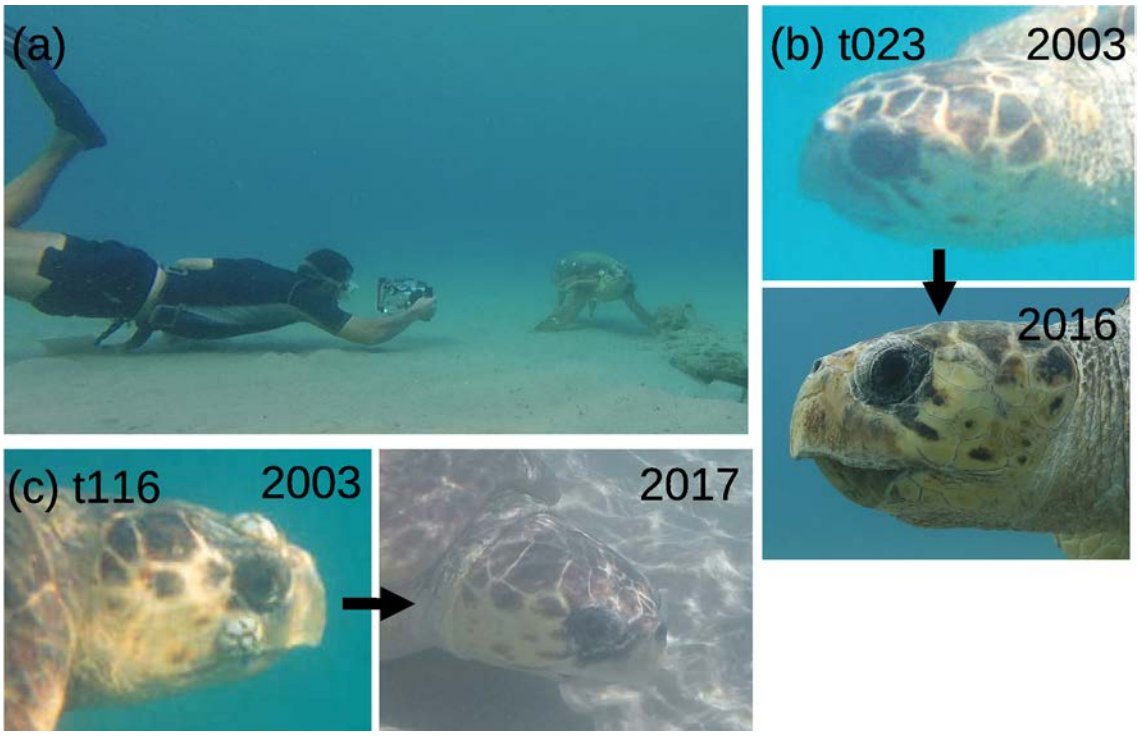
Figure legends

Figure 1 (a) Image of turtle being photographed. (b) Female turtle t116 in 2003 and 2017 and (c) Male turtle t023 in 2003 and 2016.

Figure 2 (a) Mean annual survival rates of adult female (red star) and adult male (blue star) loggerhead sea turtles at the study site in comparison to other breeding (circles; red = female) and foraging (triangles; red = female; blue = male) sites for loggerheads globally based on the number of years of surveys (data on other populations extracted from Pfaller et al. 2018; and Grossman et al. 2019). The mean annual survival rate for immature male and female sea turtles in the Mediterranean is also shown (black circle; Casale et al. 2007). (b) Estimated proportion of adult males (blue line) and females (red line) surviving different lengths of time according to the Bayesian mark-recapture model in relation to the empirical data for the proportion of males (blue dashed line) and female (red dashed line) turtles re-sighted by photo-identification (paired t-test $P > 0.05$ between modelled and empirical data for both sexes, supporting the accurate parameter estimates yielded by the models, $\hat{R}$ between 1 and 1.01).

Figure 3 Map of Mediterranean showing the destinations of 37 males and 33 females that migrated from Zakynthos. Noticeable differences were: 24% of tracked males versus 3% of females frequented sites within 100 km of Zakynthos (G test, $P < 0.001$), with several males remaining resident to the breeding area, and 38% of tracked males occupied habitat within 1 km of shore versus just 7% of females (Fishers Exact test, $P < 0.001$). Numbers represent the number of individuals at each site. The circle containing the number 7 is the location of the breeding site, Zakynthos. For the 18 tracked females from Zbinden et al. (2011), distance to shore of foraging sites information is not available, as these details were not provided in the source paper.



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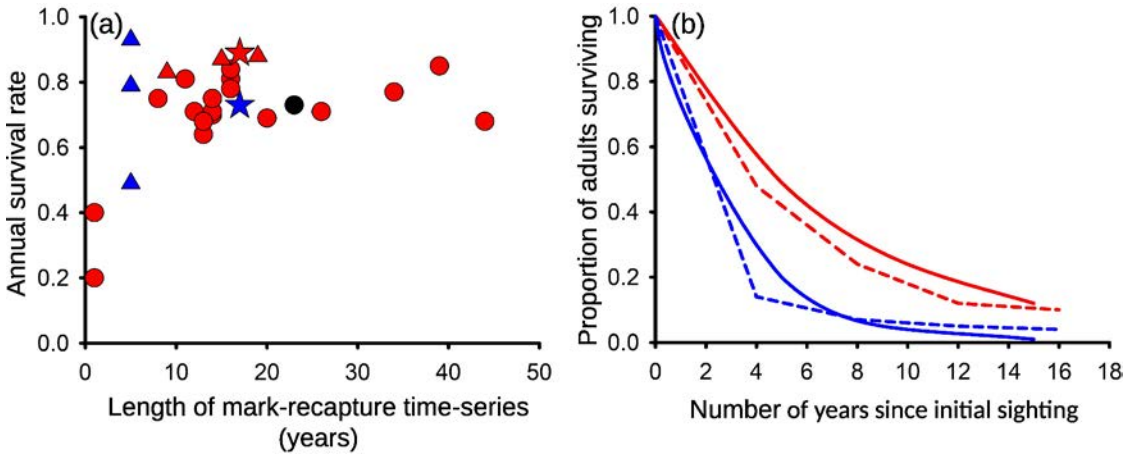

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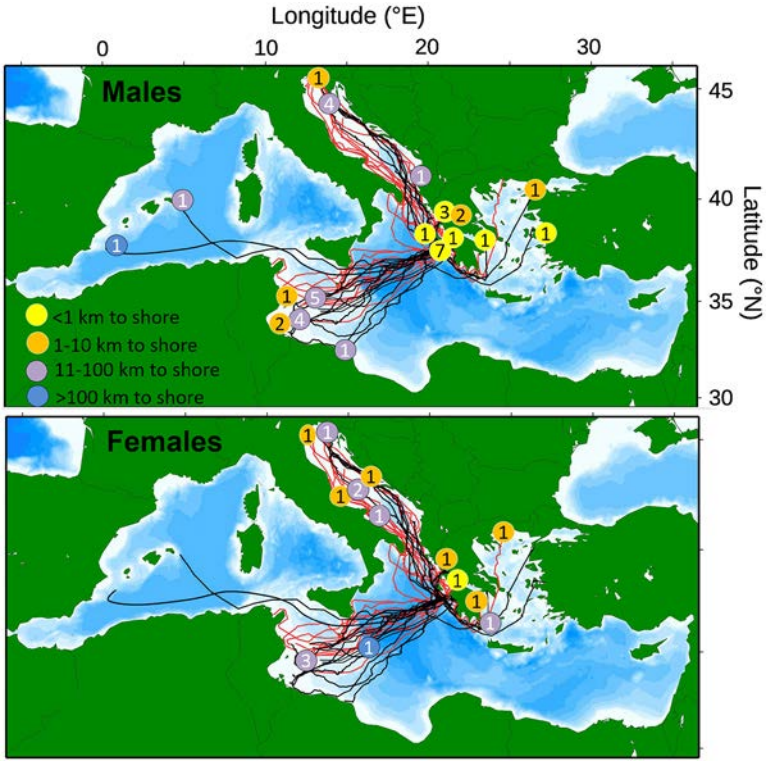

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